

## ROSIDS (MALVIDS): MALVALES

## DIPTEROCARPACEAE

**NAME:** From the genus *Dipterocarpus*, as below. The family as a whole has no common name, although in English dipterocarps in lower case implies the family broadly. A great many individual genera and species have names as treated below.

**OVERVIEW:** The family is usually regarded as comprising 17 genera and 500 species. Molecular data, while encumbered by sparse sampling of the larger genera, nonetheless demonstrates that the family as a whole is strongly monophyletic. Two small subfamilies are found respectively in Africa and tropical America while the bulk of the family consists of the exclusively Asian subfamily Dipterocarpoideae, with 13 genera and about 470 species. The subfamily shows good genus-level representation throughout tropical Asia west of New Guinea, while adding a significant pocket of endemism in Sri Lanka. The genera are individually uniform, strongly monophyletic and the molecular data generally conform to the traditional view of generic circumscription, with important exceptions in the species-rich and abundant assemblage under the tribe Shoreae which is monophyletic as a whole but finds that *Hopea* is nested within *Shorea*. The tribe requires a new structure at the genus level. (See the following separate sections on dipterocarp phylogeny and the later section on phylogeny of the tribe Shoreae.)

The best introduction to the family remains Colin Symington's classic account of Dipterocarpaceae in the Malay Peninsula<sup>1</sup>. The volume is a readable yet exact account of the many species; but more than that, it continues to inspire each new generation as a demonstration of how forest botany in the tropics should begin with the living tree. Two recent reviews of the family provide a modern account<sup>2,3</sup>. At the species level, Symington's treatment for Malaya is complemented by other good accounts for the several regions within tropical Asia; these are listed in a separate section below. No book treats the family in its entirety, nor even for tropical Asia broadly.

In stature, dipterocarps include so many species of very large size, and these are so ubiquitous and abundant, that we might wrongly conclude that the family is exclusively of the upper canopy and emergent forest layer. In *Vatica*, *Hopea* and a few types of *Shorea* we find some relatively small understory trees. Dipterocarps can be said to be without exudate but they are strongly resinous; the resin exudes slowly from cuts, often forming distinctive patches on the side of the mature trunk, sometimes strongly smelling of turpentine, while the dry resin, *dammar*, burns with a rich odor of incense. The



*Dipterocarpus alatus* planted in Ho Chi Minh City, Vietnam in the late 1890s, now with a diameter of 1.8 meters. The two trees illustrate the typical form of mature trees of *Dipterocarpus*. They make an excellent tree for urban landscape, but are rarely so used outside of Vietnam and Chiang Mai, Thailand.

presence and form of buttresses varies with genera and sections. Leaves are borne in a spiral phyllotaxy, but at maturity usually array themselves in a plane along the horizontal branches. Many dipterocarps bear glands in the leaves, although these seem to function only at the youngest stages of development. Stipules are likewise characteristic of the family and protect the growing apex in a mechanical way. The leaf stalk is conspicuous, often long and decidedly pulvinate at the blade junction. The blade is entire (*Dipterocarpus* leaves are sometimes wavy) and pinnately nerved, often with strong conspicuously scalariform venation, and varied domatia as pits and tufts. While only a few species can be said to have a densely hairy leaf surface, most dipterocarps bear some sort of hair, sometimes simple, often stellate. The typical dipterocarp flower is small in size (except in many *Dipterocarpus*), bisexual, regular, aggregated in terminal or axillary bracteate panicles, scented, with parts in fives, including a five-part calyx, often with basal tube that is persistent and distinguished by two to five of the calyx lobes that enlarge as wings in ways that are diagnostic among genera. The corolla is of five parts, more or less spiral and partially fused at the base; stamens often number 15, but vary among genera, dehiscing by longitudinal slits; the gynoecium with two to five fused carpels, styles one to three with a three-lobed stigma; ovules two to four per locule. The fruit is characteristic, a dry inde-

<sup>1</sup>Symington, C. 1943. Foresters' Manual of Dipterocarps. Malay Forest Records 16.

<sup>2</sup>Appanah, S. et al. [eds.]. 1998. A Review of Dipterocarps: Taxonomy, Ecology and Silviculture. Center for International Forestry Research, Bogor, Indonesia.

<sup>3</sup>Ashton, P. S. 2002. The Families and Genera of Vascular Plants. 5: 182-197.

Phylogeny of Dipterocarpaceae

The hypothetical phylogeny drawn below provides a linear arrangement of the genera of the Dipterocarpaceae that is similar to the traditional arrangement based on morphology, but one that incorporates the inferences from the latest molecular studies. The first efforts at phylogenetic reconstruction from molecular data were based on the chloroplast *rbcl* gene, but they suffered from sparse sampling and a choice of *Upuna* as an outgroup<sup>1-4</sup>. More recent work<sup>5,6</sup> has expanded the sampling, added other chloroplast genes (*matK* and *trnF*, etc.), and used either the Tiliaceae or *Monotes* as an outgroup. The different data sets have not been analyzed in concert, and some of the individual findings remain in conflict.

The main findings are that the Dipterocarpaceae are monophyletic at the broadest sense, including the African and South American relatives, which is not an insignificant finding in that there are no clear synapomorphies for the family. A second finding is that the subfamily Dipterocarpoideae is monophyletic, which was never much doubted. The stamens of the Dipterocarpoideae differ significantly from those in the other subfamilies, and only the Dipterocarpoideae bear significant quantities of res-

in. Likewise, the monophyly of the tribe Shoreeae (excluding for the moment *Dryobalanops*) is not surprising.

Other findings include the Sri Lankan genus *Stemenoporus* is strongly monophyletic and divergent; that *Vatica* becomes less sound with increased sampling, while the genera surrounding it are poorly resolved; that two small genera, *Upuna* of Borneo and *Vateria* from Sri Lanka, geographically isolated but with several curious similarities of form - were linked although with poor support and not supported at all by the earlier *rbcl* data. Most significantly, the tribe Shoreeae cannot be broken into monophyletic genera at the moment: *Hopea* lies nested between the white meranti (*Shorea* section *Anthoshorea*) and the rest of the genus.

The chief questions that remain include, perhaps foremost, the placement of *Dryobalanops* and *Dipterocarpus*. The study by Indrioko *et al.* (58 species, nine genera, chloroplast *rbcl*, *trnL-F* etc., with *Monotes* as the outgroup) found 95% support for the tribe Shoreeae minus *Dryobalanops* and less support for the Dipterocarpeae with *Dryobalanops* as sister. The study by Gamage *et al.* (79 species, 14 genera, *matK*, *trnL* intron and *trnL-trnF* spacer, with *Monotes* and *Tilia* as outgroups) found moderate support for Shoreeae plus *Dipterocarpus* and *Dryobalanops*. The sister position of *Dipterocarpus* is contradicted by the valvate calyx lobes and a base chromosome number of 11 rather than the seven that typifies Shoreeae. *Dryobalanops* has a base chromosome number of 7 and a fused base to the corolla, but the calyx lobes are sub-imbricate. It should be emphasized that the phylogenetic work is still early. One would like to see genes from all three components of the genome, and much more extensive sampling, and a uniform analytic method. Considering the economic and ecological importance of the family, and the ease with which material can be gathered from Botanical Gardens, such an advance should be a high priority.

<sup>4</sup>Tsumura, Y. *et al.* 1996. Theoretical and Applied Genetics. 93: 22-29.  
<sup>5</sup>Kajita T., *et al.* 1998. Molecular Phylogenetics and Evolution. 10: 202-209.  
<sup>6</sup>Kamiya K. *et al.* 1998. Tropics. 7: 195-207.  
<sup>7</sup>Dayanandan S. *et al.* 1999. American Journal of Botany. 86: 1182-1190.  
<sup>8</sup>Indrioko, S. *et al.* 2006. Plant Systematics and Evolution. 261: 99-115.  
<sup>9</sup>Gamage, D. *et al.* 2006. Genes and Genetic Systems. 81: 1-12.

	Genus or Tribe	Diversity & Distribution
?	<i>Pakaraimaea</i>	1, Guyana Highlands, S America
	<i>Monotes</i>	30, Africa, Madagascar
	<i>Marquesia</i>	3, Africa
	<i>Pseudomonotes</i>	1, South America
?	<i>Dipterocarpus</i>	75, Sri Lanka and India all of tropical Asia, especially Borneo not New Guinea.
	<i>Anisoptera</i>	11, Mainland SE Asia to New Guinea
	?	
	<i>Vatica</i>	65, Sri Lanka and India, all of tropical Asia to New Guinea
	<i>Cotylelobium</i>	6, Sri Lanka and India, Mainland SE Asia, to Borneo.
	?	
	<i>Upuna</i>	1, Borneo.
	<i>Vateria</i>	2, Sri Lanka and India.
	<i>Stemenoporus</i>	15, Sri Lanka.
	<i>Vateriopsis</i>	1, Seychelles.
	?	
	<i>Dryobalanops</i>	7, Sundaic Region (predominantly N & W Borneo), New Guinea.
	Tribe Shoreeae	191, Sri Lanka and India, all of tropical Asia & New Guinea.

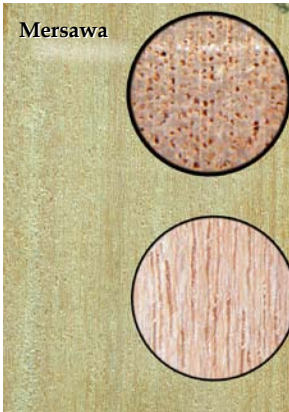
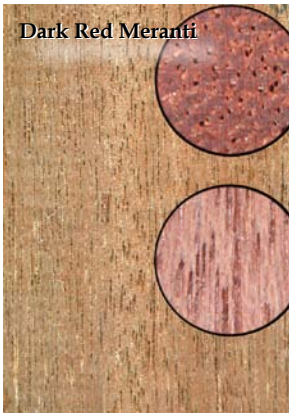
## Dipterocarps

### Timber Names and Common Names

The student grappling with the great diversity of dipterocarps will find their task encumbered by the abundance of common names for these timbers and trees, names too often conflicting or redundant or inconsistent. The name *resak* is standard Malay for species of *Vatica*, but to an Iban in Borneo *resak* is *Dipterocarpus*. This type of confusion is equally found in formal botany where common timber names and the species source were often confused: thus, the Philippine tree *mayapis* was wrongly identified with the source of *palosapis* timber, which is from *Anisoptera*, and thus confusingly named *Shorea palosapis*. The problem is further complicated by the practice of using timber names for formal botanical groups - especially for genera and sections of the tribe Shoreae - a practice that dates at least from the seminal work of Symington and a practice that is not without merit. The problem lies in talking about two or more things at once: the *balau*-group is usually meant to refer to *Shorea* sect. *Shorea*, but *balau* is also used for the exceedingly hard heavy timber that may be sourced from a variety of species from the tribe Shoreae. In this way we sometimes read, "This species produces a *balau* timber."

All that is said in the introductory essay on common names applies with particular force for the dipterocarps. In the table below, the preferred timber trade names follow from the names developed by the Malaysian Timber Trade Council and the International Tropical Timber Organization, but they are far from universally applied.

TIMBER TRADE NAME	Botanical Meaning	Common Synonyms for Timber or Trees
MERSAWA	<i>Anisoptera</i>	Philippines as <i>palosapis</i> (not to be confuse with <i>Shorea palosapis</i> which is <i>mayapis</i> ); the Iban is <i>kelapok</i> ; in Sabah as <i>pengiran</i> .
RESAK	<i>Vatica</i> , and <i>Cotylelobium</i> in Borneo.	In Borneo generally as <i>resak batu</i> ; Philippines as <i>narig</i> (but <i>narig</i> and <i>narek</i> is also for <i>Hopea cagayensis</i> ); in Kalimantan <i>giam</i> occurs, but note the preferred use below.
KERUING	<i>Dipterocarpus</i>	In Malaya <i>gombang</i> is used for the large-leaved species); <i>neram</i> for <i>D. oblongifolius</i> ; Philippines <i>apitong</i> ; the Iban is <i>resak</i> , which is Malay for <i>Vatica</i> .
KAPUR	<i>Dryobalanops</i>	<i>kamper</i> , or variant of <i>camphor</i> .
MERAWAN	relatively low density wood from some <i>Hopea</i>	Philippines as <i>manggachapui</i> (not <i>Vatica mangachapoi</i> , which is <i>narig</i> ); in Kalimantan as <i>gagil</i> (note different use in Sabah, under <i>giam</i> ); in Sarawak as <i>luis</i> and <i>tekam</i> .
GIAM	relatively high density wood from some <i>Hopea</i>	<i>Balau</i> is sometimes used in Indonesia, <i>yakal</i> in Philippines, they should be restricted to use as below; Sabah: <i>gagil</i> (for <i>Hopea sangal</i> ), <i>giam</i> ( <i>Hopea nutans</i> and <i>semicuneata</i> )
CHENGAL	<i>Neobalanocarpus heimii</i> , but sometimes applied to <i>Hopea odorata</i> , ( <i>chengal pasir</i> ), <i>H. semicuneata</i> and <i>H. ferrea</i> ( <i>chengal batu</i> )	
URAT MATA	<i>Parashorea</i>	In Sabah as <i>white seraya</i> (not to be confused with <i>white meranti</i> ); in Malaya <i>gerutu-gerutu</i> was coined in the 1930s for <i>P. lucida</i> and is still common; in the Philippines the Tagalog <i>bagtikan</i> is common, or simply <i>lauan</i> .
WHITE MERANTI	<i>Shorea</i> sect. <i>Anthoshorea</i>	Sabah: <i>melapi</i> ; Philippines <i>Shorea contorta</i> as <i>white lauan</i> ;
YELLOW MERANTI	<i>Shorea</i> sect. <i>Richetia</i>	Sabah: <i>yellow seraya</i> ; Sarawak: <i>lun</i> .
RED MERANTI	especially <i>Shorea</i> sect. <i>Mutica</i>	In the Philippines as <i>red lauan</i> or <i>tangili</i> , but see later notes under the tribe Shoreae.
BALAU	<i>Shorea</i> sect. <i>Shorea</i>	In the Philippines as <i>yakal</i> ; in Borneo generally as <i>selangan batu</i> ; <i>red selangan batu</i> for <i>Shorea guiso</i> , which in Philippines is <i>guiso</i> .



Common Dipterocarp timber, approximately natural size, original photographs of wood samples from the of the Sarawak Timber Industries Council.



## Local Area Guides to the Dipterocarpaceae

Although the Dipterocarpaceae are the most important family of plants in Asia, we have no single world-wide guide to the species, nor even a complete account for the Asian species. The individual national or regional treatments are of high quality, but are not uniform. A student looking for details of form, reference to type specimens and an account of ecology will have to cut

and paste from the different treatments. The most unfortunate aspect of the literature is how hard it can be to find a copy. Most are available in regional herbaria, sometimes as second and third generation photocopies. The following are the most important and useful works but there are many others.

### MAINLAND SE ASIA

Smitinand, T., T. Santisuk & C. Phengklai. 1980. The manual of Dipterocarpaceae of Mainland South-East Asia. Thai Forest Bulletin of Botany 12: 1-137.

Smitinand, T., J. Vidal & H. Pham. 1990. Dipterocarpaceae. Flore du Cambodge, du Laos et du Vietnam 25: 3-112.

### MALAYA

Symington, C. 1943. Foresters' Manual of Dipterocarps. Malay Forest Records 16. (reprinted by Penerbit Universiti Malaya in 1974. See revised edition, by P. Ashton and S. Appanah (2003) with updated nomenclature and distribution.)

### BORNEO.

Wood, G. & W. Meijer. 1964. Dipterocarps of Sabah (North Borneo). Sabah Forest Record No. 5. Sandakan, Sabah.

Ashton, P. 1964. A manual of the Dipterocarp trees of Brunei State. Oxford University Press.

Ashton, P. 1969. A manual of the Dipterocarp trees of Brunei State and of Sarawak (Supplement). Oxford University Press.

Ashton, P. Dipterocarpaceae. 63-388 Tree Flora of Sabah and Sarawak. 5:

### PHILIPPINES

Foxworthy, F. 1919. Philippine Dipterocarpaceae. Philippine Journal of Science. 13: 163-199.

Foxworthy, F. 1938. Philippine Dipterocarpaceae. Philippine Journal of Science. 67: 241-333.

de Guzman, E., R. Umali & E. Sotalbo. 1986. Guide to Philippine Flora and Fauna. Volume 3.

Newman M., P. Burgess & T. Whitmore. 1996. Manuals of dipterocarps for foresters: Philippines. Royal Botanic Garden, Edinburgh. 124 pages.

### FLORA MALESIANA REGION

Ashton, P. 1982. Dipterocarpaceae. Flora Malesiana, ser. 1, vol. 9(2): 237-552,

hiscent one-seeded nut with a woody pericarp, variable in size by species. Chromosome form and number has been scantily reviewed,  $x=7$  for tribe Shoreeae, and  $x=11$  for *Dipterocarpus*; the chromosomes are small and their form reveals little.

With regard to both ecology and economics it is hard to overestimate the importance of this family in tropical Asia. In stature, they include the tallest of our trees, indeed, the tallest of all tropical trees. In most lowland forests of the Sundaic Region, the family accounts for 30-50% of the trees over 30 cm DBH. Additionally, saplings often occur in large numbers and are among the fastest growing of the small woody plants. By combination of size and abundance the dipterocarps constitute the architectural framework of the tropical Asian forest.

Diversity, meaning both morphological diversity as well as species richness, is centered in Borneo where perhaps 230 species are found. Elsewhere, the number of species may be low, but their collective abundance remains high in all lowland forests of tropical Asia.

**FLORAL BIOLOGY.** It is simply astonishing to realize how little is known of the pollination and dispersal of this most important of tropical plant families. There are good reasons why so little is known, of course: these are

among the tallest of Asian trees and they flower infrequently. The subject can be concisely summarized in a few paragraphs, and it merits doing so if only to stimulate future research.

Dipterocarps are relatively uniform in floral form: a bell-shaped malvacean-type corolla, bisexual, the stamens number usually number 15 (less commonly five to 100) in one or three whorls loosely attached to the more or less basally fused corolla lobes which fall from the flower as a unit. An inflorescence is typically flower-dense and the individual flowers open singly over five to 15 days, typically dropping to the ground each morning. The flowers exude an intense volatile fragrance. The flowers seem to be without nectar, except perhaps some White Meranti and some *Dipterocarpus*. The flowers are self incompatible and obligately outcrossing. The principal variation in floral form lies in size which varies from as small as five mm to as large as five cm or more in certain *Dipterocarpus*, and also in color of the petals which varies from white and yellow to maroon, with contrasting color in the corolla throat or red-white striping on the petals.

With regard to phenology, dipterocarps exemplify two features not uncommon among canopy trees of tropical Asia in general: supra-annual masting and sequential flowering among sympatric congeneric species. Masting

refers to the habit whereby a species fruits in abundance one year which is then followed by two to six years of lesser production. The word mast, as a verb or adjective, is very old Anglo-Saxon which indicates the antiquity with which the habit was recognized, most famously among the oak trees of the Northern Hemisphere. The masting habit is fairly widespread, for example, it was found in 23% of 51 species of trees and lianas in eastern S America<sup>10</sup>. The proximal causes are complex, even in the relatively simple system of North American oaks where tree stature, weather, and reproduction in previous years all play a role, and a role that varies among species<sup>11</sup>. In tropical Asia, and especially among the dipterocarps, masting is exaggerated beyond the normal good and bad years found among the annually flowering trees of the north, for in the tropics some populations might flower only once in five to seven years. This seems especially so in forests over sandstone soils in Borneo where the entire forest appear to grow vegetatively for several years only to bloom in a wild multi-species cacophony of flower and fruit. The most famous of these events was the first to be described in much detail, the great flowering of 1955-56 over much of North Borneo<sup>12</sup>. The generality of the phenomena notwithstanding, there remains a great deal of variation and mystery about the behavior. The exact physiological mechanism by which trees obtain multi-year synchrony remains unknown.

A second phenological trait, common among dipterocarps although not restricted to the family, is sequential flowering whereby a series of congeneric and sympatric species flower in the same season one after another, rather than simultaneously. This was famously demonstrated among the species of *Shorea* in the *red meranti* group<sup>13</sup>. By some physiological trick not yet known, dipterocarps of a given species are able to synchronize their flowering with a peak period that lasts about five to seven days, each species with a peak that is separated by about a week, and each species with at least a day or so in which it is alone in reproduction. The most significant effect of sequential flowering is to allow reproductive isolation for related species living in close proximity. That effect could also be the most proximate cause in that individuals with a mutation that was linked to a shift in flower timing would immediately gain reproductive isolation from its near congener species. In this sense, sequential flowering may simply be the by-product of speciation rather than a feature driven by current competitive ecology.

Dipterocarps are pollinated by a heterogeneous range of insects. Among the small-flowered species, such as *Shorea*, thrips (Order Thysanoptera) were found to breed within the flower buds and feed on the petals<sup>14</sup>. After

the flower blooms at night, the thrips fall to the forest floor along with corolla, then return to the canopy along with whatever pollen remains stuck to their body. Factors that mitigate against thrip pollination are the great vertical distances between forest floor and canopy and the great horizontal distances between trees of the same species, the weak flying ability of thrips, the lack of any special pollen receptacle, the night-blooming of the species (other thrip-pollinated species are day-blooming), and the destination of the thrips which is another flower bud rather than an open bloom with a receptive stigma. Comparative studies in Sarawak showed that while thrips were present they were largely irrelevant to pollination and the pollen vectors there were beetles which feed on the corolla<sup>15</sup>. The issue deserves much further comparative study.

Medium-sized flowers such as *Dryobalanops* are visited by *Apis* and *Trigona* bees. The large-flowered species of *Dipterocarpus* may have a more varied array of pollinators<sup>16,17</sup>. *Dipterocarpus obtusifolius* blooms at dusk and secretes nectar for 24-36 hours while attracting large moths (Sphingidae and Noctuidae). During the following day they also attract butterflies (primarily Pieridae and Papilionidae), and even birds, and also we might presume *Apis* bees if available.

**DISPERSAL.** The fruit of most species of Dipterocarpaceae bear a single fairly large seed, from 5-25 mm across. The fruit is subtended by the calyx lobes, 0 to five of which expand as wings that range up to 20 cm in length. One mystery of dipterocarp dispersal lies in the apparent contradiction of winged fruit that either do not fly at all or fly clumsily no more than 10-40 m from the mother tree. If by 'wind-dispersal' we mean a fruit or seed that floats on the lightest breeze, as in a dandelion or the plumed seeds of many Apocynaceae, then dipterocarps certainly fail to conform. One hypothesis, rarely advanced and never investigated, is that the wings function in wind dispersal but only in the strongest of winds. Such winds occur once or twice a year during the time of transition from NE to SW monsoons. This is a time of tremendous thunderstorms when great thundering gusts of wind develop, winds strong enough to knock down a hectare or more of forest. In this scenario, the fruit wings are effective only in those occasions when mature fruit meets the strongest of winds, an instance that - while rare - nonetheless effects a high chance of success for the resultant seedling.

Most genera show a correlation between fruit size and wing development<sup>18</sup>. Wingless fruit appear to be secondarily derived and repeatedly so within the genera *Dipterocarpus*, *Vatica*, *Shorea*, *Parashorea* and *Hopea*. The occurrence of wingless species is associated with two ecological habits. First, are the riverside and swamp species in which the fruit are evidently adapted for water dispersal. Second, are species of smaller stature of the forest understory. These are almost without exception geographically localized species, and in some cases represent local small-statured species presumably derived

<sup>10</sup>Norden, N. *et al.* 2007. PLoS ONE 2(10): e1079.

<sup>11</sup>Sork, V., *et al.* 1993. Ecology 74: 528-541.

<sup>12</sup>Wood, G. 1956. Malayan Forester. 19: 193-201.

<sup>13</sup>Chan, H. *et al.* 1980. Malayan Forester. 43: 132-143.

<sup>14</sup>Appanah, S. *et al.* 1981. Malaysian Forester 44: 234-252.

<sup>15</sup>Sakai, S. *et al.* 1999. American Journal of Botany. 86: 62-69.

<sup>16</sup>Ghazoul, J. 2004. Biotropica. 36: 156-164.

<sup>17</sup>Ghazoul, J. 1997. Journal of Natural History. 31: 901-916.

<sup>18</sup>Suzuki, E. *et al.* 1996. Journal of Tropical Ecology. 12: 853-870.

from species that are widespread, large-statured, and bear winged fruit.

A third class of wingless seed is represented by *chengal* (*Neobalanocarpus heimii*) which differs from the other classes in that it is a species of dry forests, is exceedingly tall, patchily widespread in the Malay Peninsula, and taxonomically isolated. The large single-seeded fruit behaves very much like an acorn and the dispersal may be likewise effected by scatter hoarding ground mammals.

**ECONOMICS.** The family contributes a wide variety of resins, as well as the illipe nuts. A few species are planted as shade trees. However, the chief economic value of the Dipterocarpaceae derives from the timber that has contributed uncounted billions of dollars to the national economies of tropical Asia. The literature on the timber trade, its management and mismanagement is very large and nothing more will be said here other than to give some idea of the scale. According to Malaysia Timber Council statistics, in 1997 Malaysia exported about 13 million cubic meters of logs, sawn timber and plywood earning 60% of the total US\$ four billion in export wood trade. In 2007, the export volume was down but earnings up with 11 million cubic meters of logs, sawn timber and plywood earning 50% of US\$ 6.5 billion. A volume of nine million cubic meters equals a block of wood one m thick and three km by three km square. Those figures are only for Malaysia, which is second only to Brazil in the global business of timber. Note that most of the other nations of tropical Asia, once timber exporters, are now timber importers. For further reading on timber economics and how and why a rise in the value in a natural resource can lead to the collapse of its sensible management, the volume by Michael Ross can be recommended highly<sup>19</sup>.

**DIPTEROCARPUS.** [Greek two-winged fruit.] A genus of 75 species distributed from Sri Lanka to the Philippines, about 50 species in Borneo, 30 in Malaya. Typically, two or three species will be abundant in any particular forest. Within the dry-seasonal parts of tropical Asia we find fewer species but they remain of great ecological and economic importance.

The genus differs from other dipterocarps in that the calyx is fused as a tube and two calyx lobes develop as wings, although a few species have no wings at all. Vegetatively, the genus is relatively homogeneous. Almost all are big columnar trees with either plank buttresses or low round buttresses. The bark is a distinctive light brown, flaking in large or small sheets or plates, not furrowed. A few species of the fire-prone dry-seasonal lands of Mainland SE Asia have a dark, thickly furrowed bark. The leaves are diagnostic in their folded surface and wavy edges, and leaf stalk is strongly swollen at the top. The blade is thick and stiff and resistant to decay, easily found beneath the tree; some are small, a few hairy, many

are large and stiff like a fan; they may bear some resemblance to some species of *Dillenia* in the very straight regular nerves and the wavy margin, but *Dillenia* has a very different leaf stalk and node. The stipules are significant in several respects. Unlike most dipterocarps where the stipule covers the growing leaf before it emerges, in *Dipterocarpus* the stipules at one node cover not the leaf itself, but the next younger leaf. The stipules vary in ways that are often diagnostic for the species: they can be pale golden or red, and variously hairy sometimes with clusters of long hairs. They fall away from apex as the leaves unfold in a great flush of new growth and are often scattered beneath the tree like banana peels. Note that the stipules often differ in form depending on the time of production and may differ greatly between adults and juveniles. The leaf stalk is always swollen and bent where it joins the leaf base.

In perhaps a quarter or more of the species the sterile leaves can be recognized to species. However a great many species are so similar in leaf form that fruit are required to confirm the identity. The mature fruit is highly variable among species in detail: size, shape, ridges, shoulders, and so on. In contrast, the flowers, while larger than other dipterocarps, vary only a little among species.

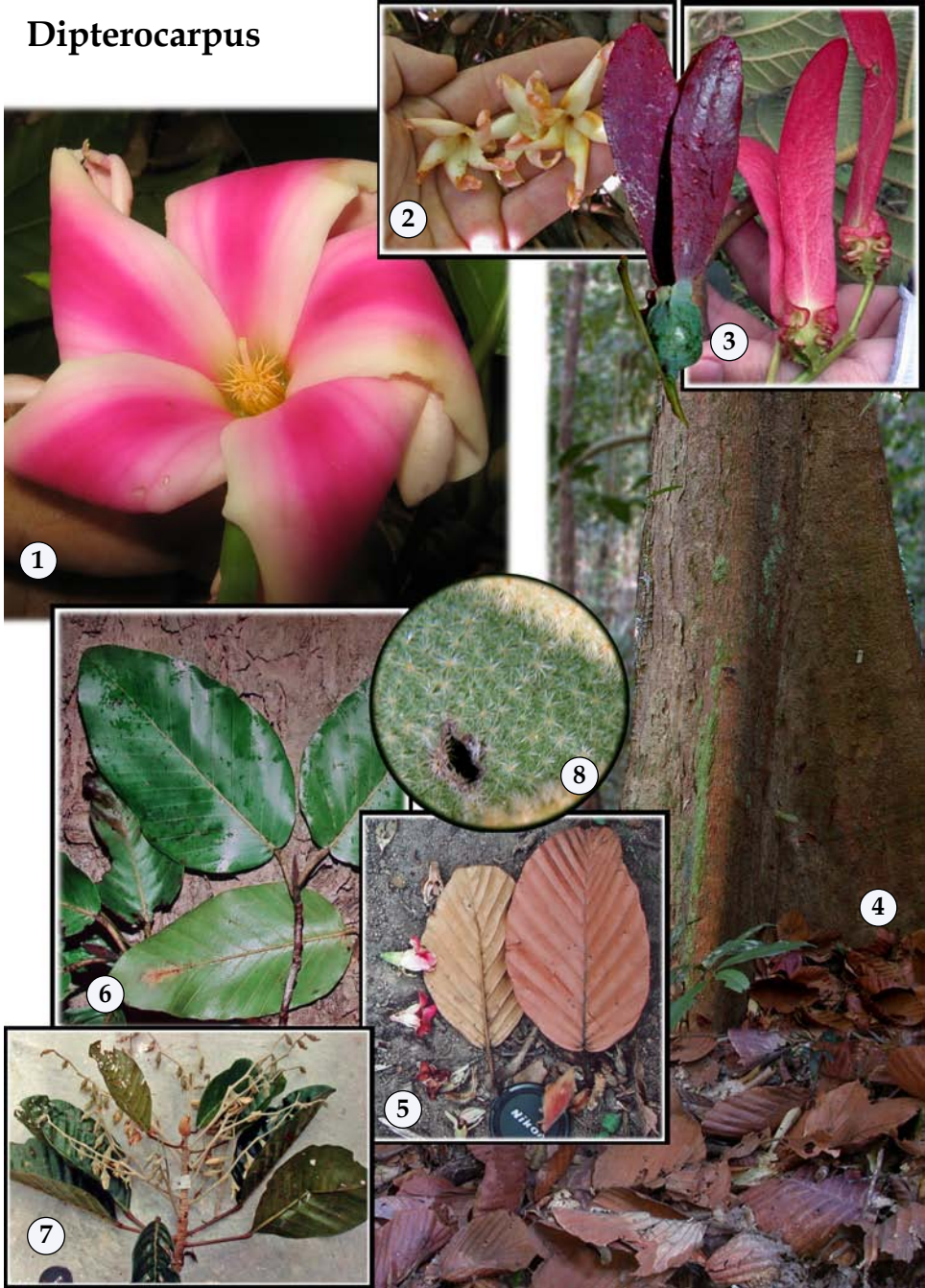
*Dipterocarpus* species are common in all primary lowland forests with the exception perhaps of peat and kerangas. In ecology, most species can be considered wind dispersed, light demanders, regenerating patchily, and often forming dense clusters of saplings a hundred meters or so about the mother trees. Efficient water transport in the xylem is afforded by the relatively wide and long xylem vessels. They may play a greater role in the early development of forest structure than is often recognized, depending heavily on disturbance associated with ridges and stream valleys. They seem to be generally intolerant of very wet soils, but nonetheless are often enough found nearby streams, perhaps depending on them for the forest gaps that follow as the water floods and changes course.

Species of *Dipterocarpus* flower annually or supra-annually; some species will flower twice a year. The flowers of the inflorescence bloom singly over several days to a week or more depending on species. In many species the flowers open in the late afternoon, just before sunset, and remain open through latter part of the following morning with visitation at night (especially hawk moths and *Apis* bees) and a diversity of day insects. A rich somewhat cloying sweet perfume is characteristic, and at least a few species produce nectar from the base of the petals.

Besides furnishing timber, the trees have since ancient time been tapped for their resin. From Myanmar to Borneo and the Philippines, people tap the trees in much the same manner. A large hollow is made in the side of the tree near its base. After a time resin builds up in the apex of the hollow and it is removed by fire.

<sup>19</sup>Ross, M. 2001. Timber booms and rent seeking in Southeast Asia. Cambridge University Press.

# Dipterocarpus



*Dipterocarpus*. 1, flower of *D. grandiflorus*, Philippines, showing the five overlapping corolla lobes, clustered stamens and central exerted style; 2, flower of *D. crinitus*; 3, the fruit of *Dipterocarpus* is distinctive with the two calyx lobes expanded as wings, often red before drying, species vary in the length of the wings, size of the seed and details of the calyx with regard to ridges and wings; 4, *D. confertus*, 86 cm DBH, large columnar trees with low plank buttresses and a dense bed of persistent dry leaves around the base; 5, the dry leaves are distinctive in the strong regular nerves that nearly touch the wavy margin and the plicate leaf surface, 6, the fresh leaves can appear more pliable; 7, the inflorescence is often sparsely flowered in arrays of axillary racemes; 8, indumentum when present is often in star-shaped clusters. (Photograph 1, © Ulysses Ferreras.)



# Dipterocarpus



*Dipterocarpus*, diversity of form. 1-3, *D. acutangulus*; 1, low buttressed trunk with shaggy bark, 80 cm DBH; 2, small leaves, finger for scale, with sharply ascending nerves; 3, juvenile twig with bristle-bush apex; 4, *D. caudatus*, trail side tree at Bukit Timah, Singapore, with low plank buttresses, smooth elliptic leaf; 5-6, *D. geniculatus*; 5, columnar trunk, still immature at 35 cm DBH, with distinctive flaking bark; 6, the dry leaf with long geniculate leaf stalk (see inflorescence of the same species on previous plate); 7-8, *D. cornutus*; 7, pale columnar trunk with low buttresses, 89 cm DBH, the inset showing the large strongly nerved leaf and red-winged fruit; 8, the stipule of the juvenile is diagnostically long, pendent and bears clusters of golden stellate hairs; 9, the twig apex of *D. kunstleri* juvenile, long smooth and differs from the adult which bears large paired stipules like banana peels; 10, *D. grandifolius*, with typical columnar bole and pale tan flaky bark (arm for scale), inset of fallen leaf and fruit; 11, *D. crinitis*, 131 cm DBH, distinctive in the broad base, rounded nearly fluted buttresses.



*Dipterocarpus intricatus*, Vietnam, the thick, dark, deeply ridged bark is characteristic of several *Dipterocarpus* species found in dry-seasonal lands, especially in places prone to fire; however, it is very different from the bark typical of the lowland equatorial species of the Sundaic Region.

**ANISOPTERA.** [Greek, unequal-wings.] A small genus, but abundant, with 12 species distributed from Bangladesh and Myanmar, to Malaya, Sumatra and Borneo, north to Luzon and east to New Guinea, but absent from the Lesser Sunda Islands.

*Anisoptera* shares with *Dipterocarpus* a calyx tube that covers the fruit and two-wings joining the fruit at its

apex. But in *Anisoptera*, the calyx wall is tightly fused to the fruit wall. Furthermore, the leaves differ in the looped venation and the smooth, rather than folded, surface, and in the peltate hairs which *Dipterocarpus* lacks. Although long linked to *Dipterocarpus*, the molecular studies cited all indicate that *Anisoptera* is more closely related to *Vatica*.

Species differ in details of the style and number of stamens, as well as gross features of the leaves and bark. The fruit are fairly uniform.

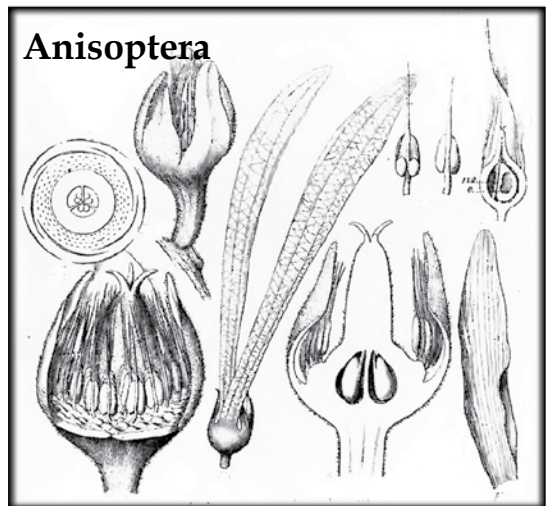
There are two basic kinds of *Anisoptera* representing what are two sections of the genus: Section *Glabrae* is represented by *A. laevis* and relatives with a smooth gray bark, twig tips essentially glabrous and the buds relatively broad. Section *Anisoptera* is represented by *A. costata* and the bulk of the species in which the bark is brown, more or less shallow fissured with flaking ridges, the young parts of the twig

all with the long hairs, and the buds narrow and pointed.

These trees are often on ridges, sometimes in small groups but rarely with gregarious saplings. It seems that this genus, perhaps even more than other dipterocarps, is subject to insect predation of the seeds. It is suggested that the seedlings are strong light demanders. The seedlings of *A. thurifera* in New Guinea germinate before falling, that is, they are viviparous in the manner of *Rhizophora*, an unusual feature in dry forest trees. And this species more than any other is a relatively aggressive colonizer, regarded in the Philippines as the only dipterocarp that can invade deforested land. The seeds of *A. thurifera* are gathered and eaten in northern Luzon, in the fashion of illipe nuts.

**VATICA.** [Linnaean name from Latin *vaticanus* prophesy or *vates* a prophet in reference to use of resin for incense.] About 65 species, one of the most widespread of dipterocarp genera, well-represented in India, Sri Lanka and eastward in Mainland SE Asia, and especially in the Sundaic Region, seven species north into the Philippines, only *Vatica resak* west to New Guinea.

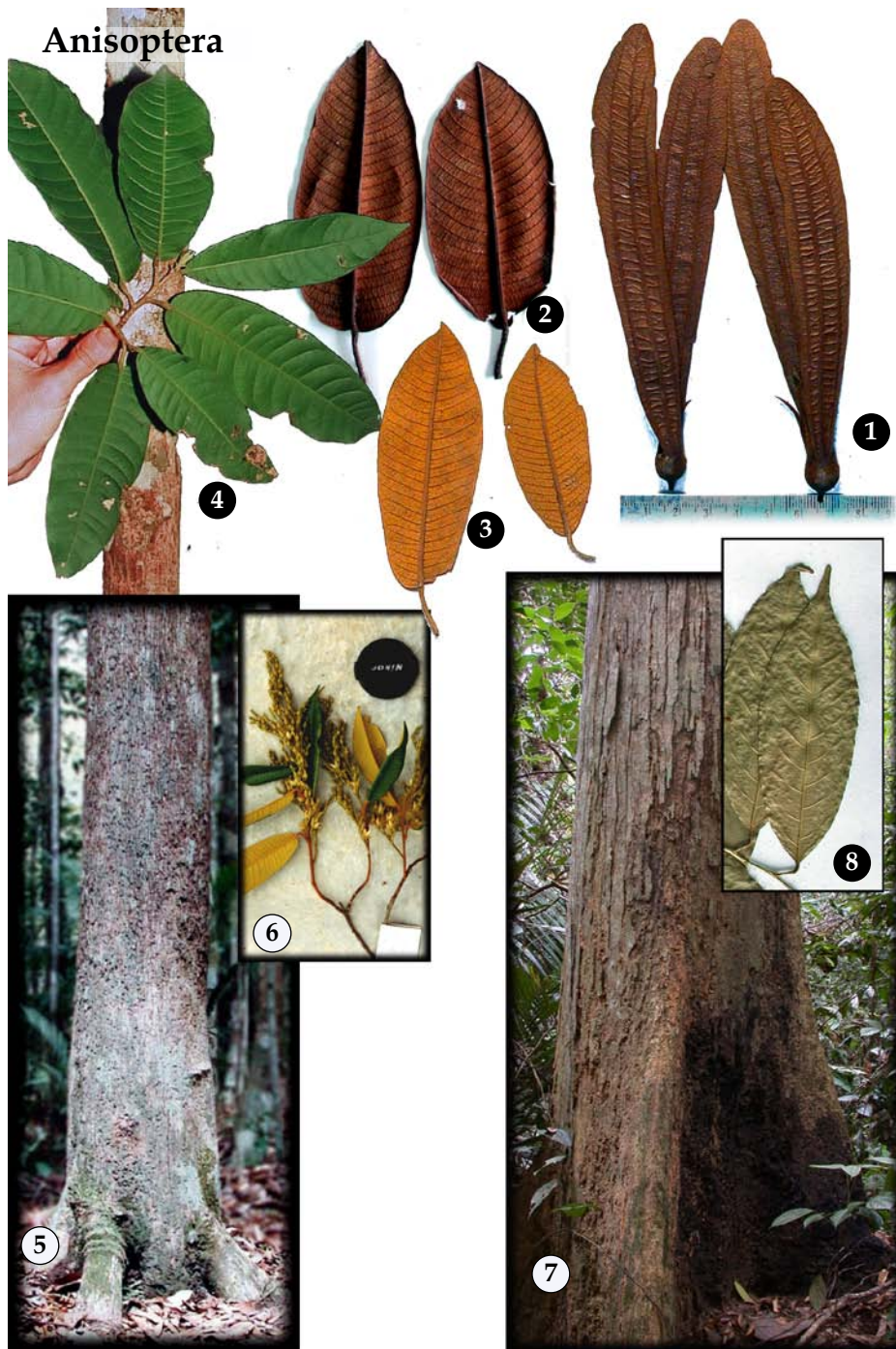
*Vatica* species are generally uniform in vegetative and floral features. They are often small to medium trees with smooth gray bark most always with distinctive hoops along the bole. A few species reach large diameters, especially in the dry-seasonal lands, but never great heights. Most species of *Vatica* bear glands at the extremities of the major nerves in the leaf blade; these glands are generally longer than wide and conspicuous in both fresh and dry leaves. The dry leaves of some species can be mistaken for *Parinari* (Chrysobalanaceae) because of those glands. The stipules of *Vatica* vary greatly in size and persistence from very large to almost negligible. In some species of *Vatica* the stalk is somewhat twisted and the entire twig has a messy appearance which contrasts with



*Anisoptera*. Floral and fruit details, drawing adapted from BLUME loc. cit.



# Anisoptera

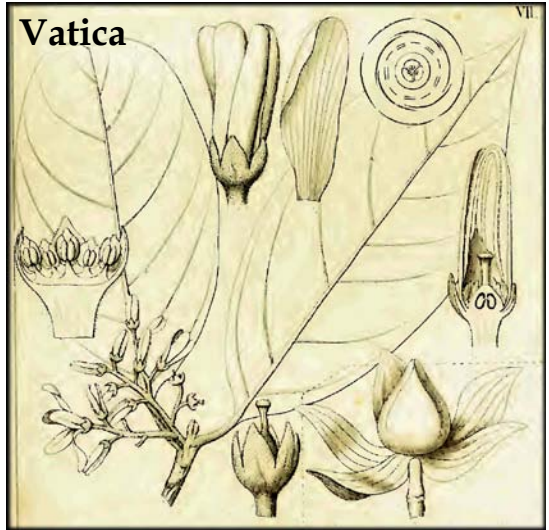


*Anisoptera*. 1, fruit with two extended calyx lobes as wings; 2-3 dry leaves, lower surface, nerves characteristically strong, regular, spreading and looped near the margin; 4, *A. costata* sapling, the leaves with long pulvinate stalks, the 3 cm DBH tree behind; 5-6, *A. grossivenia*, 65 cm DBH, with typical columnar bole and short broad buttresses, the leaves of the mature tree are small, golden below, the inflorescence dense with small lowers; 7-8, *A. laevis*, 67 cm DBH, with a contrasting form and bark, the leaves thin and papery, the nerves thin and arched.

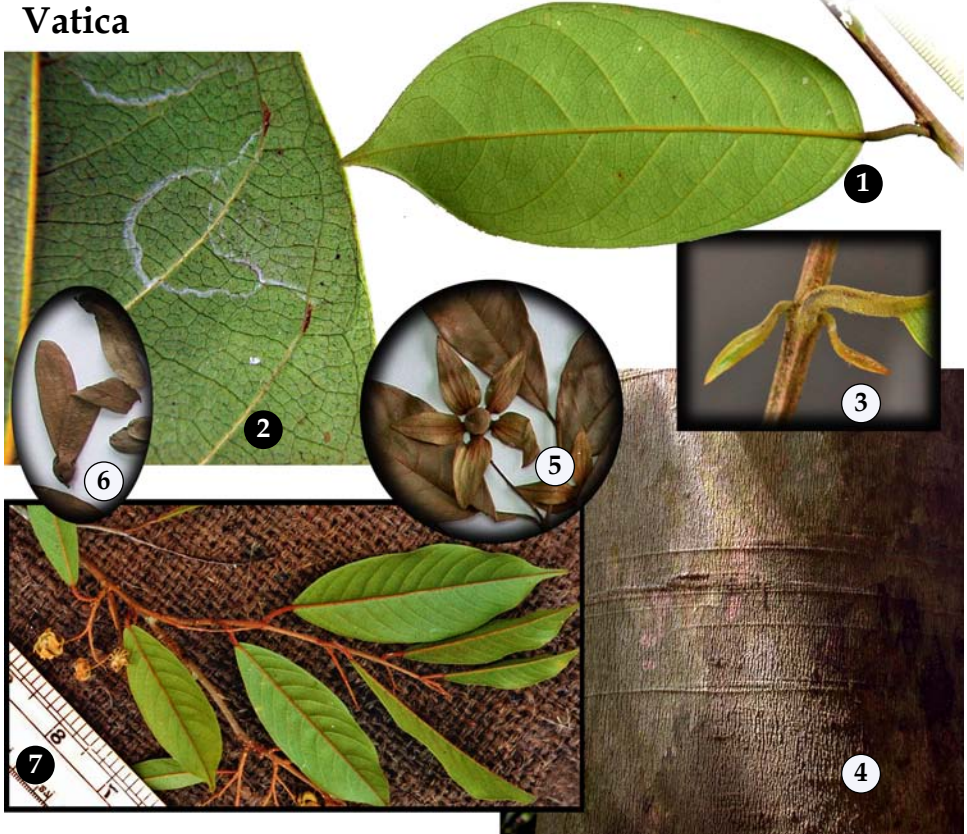
the normally neat and clean twig habit of most dipterocarps. The flowers are also generally uniform among species, with 15 stamens, four-celled anthers and the ovary slightly embedded in the calyx tube. It is in the fruit that the genus varies most significantly. The two main types are a fruit with equal calyx lobes, either as small wings or little more than stumps or with calyx lobes strongly unequal, usually two longer than the other three. Many species share similar leaf form and encompass sufficient regional variation to hinder recognition on leaves alone, but with fruit specific identification is not difficult.

These are common and consistent lowland forest trees that perhaps become increasingly abundant with elevation and slope, sometimes richly aggregated on ridges. Some species seem to favor stream sides; they are not known to be invasive or weedy.

It is interesting that notwithstanding the general opinion regarding the uniformity of the genus, the molecular studies cited in the family



*Vatica pauciflora*, details of flower and fruit, illustration adapted from BLUME *loc. cit.*



*Vatica*. 1-3, *V. pauciflora*; 1, leaf blade with arched nerves regular nerves, but weakly scalariform venation, and a sinuous stalk; 2, the weakly scalariform to reticulate venation is scarcely raised, while laminar glands are found along the main nerves near the margin; 3, paired stipules fall away early; 4, the typical bark is gray, tight, smooth and with strong horizontal hoops; 5-7, three types of fruit; 5, with equal calyx lobes as expanded wings; 6, with strongly unequal calyx lobes, here with two wings; 7, with equal calyx lobes shortened as mere stubs.





*Cotylelobium melanoxylon*; the trunk with low rounded buttresses, black scaly bark; the leaf with distinctive nerves and veins.



discussion found low level of support for the monophyly of *Vatica*, in contrast to the 90-100% bootstrap support that characterizes *Dipterocarpus*, *Anisoptera*, *Stemenoporus* and so on.

The wood is close grained, pale, and resinous. It carves well, but has been of little use in the past.

**COTYLELOBIUM.** [Greek, the cup like cavity and seed.] A genus of five species, with one in Sri Lanka and four in the Sundaic Region, and especially in Borneo. The general form and ecology of *Cotylelobium* falls within the range of *Vatica* as the common name *resak batu* would imply. The leaf venation is distinct for each of the species.

**UPUNA.** [From the native Iban name *upün*.] Monotypic, *Upuna borneensis* is an evidently isolated taxon, restricted to west Borneo, but bearing similarities with two Sri Lankan endemic genera, *Stemenoporus* in some floral features and *Vateria* in a similarity of leaf form. Molecular evidence, not strong, further links the three genera. In Borneo, *Upuna* is quickly segregated from other Dipterocarps by the medium-sized leaf with a cordate base and white tomentose undersurface. The calyx forms a distinct cup free of the nut, the lobes are valvate with two lobes much longer than the other three and

## Dryobalanops



*Dryobalanops*. 1, *D. aromatica*, this example of only medium diameter but already tall with characteristic bark; 2-4, drawings of flower and fruit; 5, fallen leaf and fruit of *D. beccarii*; 7, flowering branch of *D. aromatica*; 6, fallen leaf of *D. lanceolata*. All photographs from Lambir, Sarawak; drawings adapted from BAILLON *loc. cit.*

the pericarp of the three-angled nut splitting at maturity with basal collar akin to a rudimentary aril.

**DRYOBALANOPS.** [Greek, oak or by extension tree, and *balan*, acorn.] A small but locally abundant genus of seven species, all seven in Borneo where they are chiefly in lowland forests but also on white sands and in peat swamps. They are sometimes gregarious and can comprise a large portion of the canopy. Two species are found in Sumatra and along the east coast of Malaya but not elsewhere in the Peninsula. The name *kapur* is standard.

The flowers are fairly large, with spreading white petals and 20 to 30 stamens. These are big scaly-barked trees, sometime of enormous proportions with great sharp buttresses and a yellow-black dammar. The leaves are relatively small with distinctive venation, appropriately termed 'dryobalanoid'. The stipules are very small and fall quickly. The plant body is strongly resinous; form the pungent odor the genus can be distinguished from those species of *Hopea* with similar leaves, such as *H. dryobalanoides*.

The adult trees are huge emergents that regularly flood the surrounding forest with saplings that are of-

ten so numerous that they easily dominate the understory. The largest adults are magnificent towers of wood, crowning the forest ridges and standing high above the canopy. Each species tends to require a special combination of soil, moisture and topography, which have yet to be made explicit. One exception is the contrast between *D. aromatica* which is exclusively on sandstone soils and *D. lanceolata* which is restricted to richer clay and shale soils. The complementary distributions, which display a remarkable fidelity to even small soil patches, are beautifully illustrated in the Lambir 52-ha plot distribution maps. The flowering of *Dryobalanops* appears to be at fairly regular intervals, the flowers primarily open at day and visited by *Apis* bees.

*Kapur* timber is of sound quality and generally similar to most other dipterocarps, but kapur is of special significance to the timber man because of its excellent traits suitable for rapid growth in either plantations or through silvicultural manipulations. It is among the faster growing of dipterocarp species achieving over one cm DBH per year in forest conditions. The fast growth of kapur can be seen in the plantations at the Forest Research Institute of Malaysia in Kepong. Since first planted in 1930s they have yielded about five-six m<sup>3</sup> of timber per ha per year.

## #

### ☪ - *Shorea* Group - ☪ Tribe Shoreae\*

The many species of the tribe Shoreae have a reputation for taxonomic difficulty that is not quite accurate. In fact, a student can master the recognition of the majority of species from leaf and bark alone, so long as they are willing to walk the forests armed with a good eye for the details of vegetative form and acquire the necessary field experience. Any student should understand that the confusion so often attributed to the tribe Shoreae stems from two key features. First is the more than 200 species involved and their rough similarity: simple alternate sipulate leaves. Second is the peculiarity of distribution and ecology whereby the most abundant species in any particular location may be unknown anywhere else. For example, at Lambir in Sarawak, the most abundant species of *Shorea* was *S. acuta*, a species known only from a small area on the west coast of Borneo. The three plots of Lambir, Pasoh and Palanan included about 90 species of the tribe Shoreae, of which only nine species were found in more than one plot. This pattern of distribution demands considerable travel and time to gain field experience with the rich diversity of the tribe.

As a group, these trees are distinguished by the calyx, which subtends the ovary rather than being fused to it, and bears lobes that overlap. About six genera have recognized in most current treatments, but numerous other genera have been named in the past. While the entire tribe appears to be monophyletic, the molecular

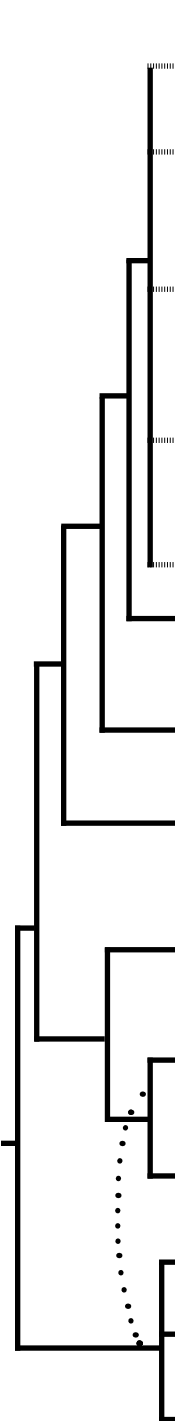
data to date implies that *Hopea* is nested within a broad *Shorea*, bracketed on the one side by the White Meranti Group (*Shorea* Section *Anthoshorea*) together with the Sri Lankan *Doona*, and on the other side by the other Meranti groups. Also, some of the smaller genera indicate potential problems. These include the status of *Neobalanocarpus* as a putative cross-generic hybrid, and a lack of uniformity in the former genus *Pentacme*. Plausibly, the entire tribe could be treated as a single large genus, however such a broad lumping, while philosophically righteous, would include a vast array of diversity in contrast to the relatively more uniform genera such as *Dipterocarpus* and *Dryobalanops*, it would cause confusion in the creation of new binomials for well-known species, and generally contribute nothing to either understanding or practice. The more sensible choice is to divide *Shorea* into segregate genera, a project that will have to await a more comprehensive survey of molecular data. Such a survey is certainly justified among what are the most economically important of all Asian trees. For now, I follow the conventional practice of using informal names for the monophyletic groups while leaving the traditional binomials intact. Maury-Lechon provides an thorough review of the tribe<sup>20</sup>.

**SHOREA.** [Commemorates Sir John Shore, d. 1834, Governor-General of India.] Altogether including some 196 species with a broad tropical Asian distribution from India and Sri Lanka to New Guinea and the Philippines.

\*Following the recommendation of James Reveal, and contrary to the common spelling with a single internal 'e', the tribal ending of -eae should be added to the base Shore to make Shoreae.

<sup>20</sup>Maury-Lechon, G. et al. 1998. in A Review of Dipterocarps: Taxonomy. pages 5–44.

Phylogeny of Tribe Shoreeae

Genus or Group		Description	Diversity & Distribution
	Ovalis Group <i>Shorea</i> sect. <i>Ovalis</i>	50-70 stamens, connective without appendage, ovary with short style, hairy, large inflated stipule, fissured bark.	1, <i>S. ovalis</i> , Sundaic Region.
	Nemesu-tangile Group <i>Shorea</i> sect. <i>Brachypterae</i>	15 stamens (1 sp. 22-26), long aristate extension of connective; long style with a constricted base or pubescence, some with strong persistent stipules; bark scaly not fissured (except <i>S. smithiana</i> ).	24, <i>S. pauciflora</i> , Sundaic Region, <i>S. smithiana</i> & <i>S. fallax</i> , Borneo, <i>S. almon</i> , <i>S. polysperma</i> & <i>S. palosapis</i> Philippines, 1 east to Maluku.
	Mutica Group <i>Shorea</i> sect. <i>Mutica</i>	15 stamens, appendage shorter than the anther, often reflexed, ovary hairy, style more or less equal length to ovary; stipules moderate size, not usually persistent; many with bark deep V-fissured, but some species smooth barked, ( <i>S. macroptera</i> ).	26, <i>S. leprosula</i> , <i>S. curtisii</i> , <i>S. acuminata</i> & <i>S. macroptera</i> Sundaic Region, absent from Lesser Sunda Islands, not north of Malaya, absent from Palawan & Mindanao.
	Illipe Nut Group <i>Shorea</i> sect. <i>Pachycarpa</i>	15 stamens, appendage slender, longer than anther, small ovary and small slender style, mostly glabrous, large persistent stipules, bark smooth, hooped, flaky at full maturity.	9, <i>S. macrophylla</i> , <i>S. amplexicaulis</i> / <i>S. beccariana</i> Borneo,
	Negroensis Group <i>Shorea</i> sect. <i>Rubella</i>	15-50 stamens, appendage shorter than anther, anther linear, bark of white meranti, wood of Mutica-type.	5, monophyletic?, nested within Mutica?, <i>S. albidia</i> Borneo, <i>S. negrosensis</i> Philippines,
	Balau Group <i>Shorea</i> sect. <i>Shorea</i>	stamens 20-60, connective with short bristly appendage (unique in tribe), hairy ovary; small stipules, flaky or dippled bark, hard heavy wood.	About 40, <i>S. robusta</i> (sal tree) India, <i>S. maxwelliana</i> , <i>S. laevis</i> , Sundaic, <i>S. guiso</i> & <i>S. falciferoides</i> Sundaic and Philippines.
	Yellow Meranti Group <i>Shorea</i> sect. <i>Richetioides</i>	2-celled anthers, 15 (10) stamens, ovary hairy, stipules minute, fugaceous, bark scaly.	32, aseasonal tropical Asia including Philippines, <i>S. faguetiana</i> , <i>S. multiflora</i> , <i>S. gibbosa</i> , <i>S. laxa</i> .
	Parashorea GROUP	4-celled anthers, 15 stamens, blade glaucous below, many with nerves at strong angle to midrib; corolla white to yellow, wings 5 equal short or long, or three long, two short.	13, Mainland SE Asia, Malay Peninsula, Sumatra, Borneo, Philippines.
	Hopea sect. <i>Dryobalanoides</i>	15 stamens (or 10 <i>H. treubii</i> ); dryobalanoid venation; bracts fugaceous, corolla pale; ovary and stylodium ovoid or ; bark smooth, fissured, cracked, not flak; always 2 long calyx lobes as wings.	23, Mainland SE Asia to Borneo and Philippines, <i>H. malibato</i> .
	Chengal <i>Neobalanocarpus heimii</i>	Like the scalariform-leaf <i>Hopea</i> as below, but anthers oblong with a short squat appendage, 5 short but unequal calyx wings; lamina base unequal.	1, <i>Neobalanocarpus heimii</i> , Malaya.
	Hopea sect. <i>Hopea</i>	15 stamens (or 10, <i>H. sangal</i> ); nerves scalariform, lamina base equal or unequal, always 2 long calyx lobes as wings.	46, Sri Lanka and India, to Mainland SE Asia, Malaya, Borneo, Philippines and 10 in New Guinea. <i>H. odorata</i> , <i>H. acuminata</i> .
	White Meranti Group <i>Shorea</i> sect. <i>Anthoshorea</i>	15 (or 30) stamens, yellow laminated inner bark, large stipules, broad corolla, fruit with three wings (or 0).	<i>S. roxburghii</i> , <i>S. bracteolata</i> , <i>S. javanica</i> , <i>S. ochracea</i> , <i>S. assamica</i>
	formerly <i>Pentacme</i>	15 stamens, 4-celled anthers, large cream colored flowers, stipules small, fugaceous, bole V-fissured, wood, fruit with three wings.	<i>S. siamensis</i> , <i>S. contorta</i> .
	<i>Doona</i>	fruit with three wings	Sri Lanka

It is described below in the order of constituent groups as presented in the phylogenetic chart.

**A -- *Shorea ovalis* -- a**

The group is usually regarded as a singular species, *Shorea ovalis*, most widely known by the Malay *meranti kepong* but with local names wherever it grows. It is widespread and common in the Sundaic Region, unusual in the numerous stamens (50-70); recognized in the field from the curled boat-shaped dry leaves on the ground, the blade with many strong nerves and scabrid surface, and the inflated and constricted stipules of the juveniles. In the Philippines, it should not be confused with *S. palosapis* which has similar looking stipules. Despite what has long been considered to be its relatively uniform and readily recognized appearance, the most recent molecular study of *PgiC* gene by Kuoya (cited above) implied polyphyly, with individuals scattered across several clades within the *Rubroshorea* group. However, in that study, *S. ovalis* was not the only species where multiple samples failed to match in sister position. Consequently, I would tend to regard the species definition and phylogenetic placement of *Shorea ovalis* as an open question.

This group of about 24 species is equivalent to the traditional section *Shorea* sect. *Brachypterae*, distinguished by: (1) a distinct constriction or at least a dense pubescence at the base of the style (stylopodium); and (2) scaly rather than fissured bark (except for *Shorea smithiana*). These are common and abundant trees especially in the Sundaic Region, but also important timber trees of the Philippines where it yields *red lauan* and *tangile* timber. The Philippine common names have become badly muddled as the supplies of timber dwindle. In particular, the name *tangile* is now widely used for almost any sort of light red timber, and since more than a small supply comes off ships from Borneo, it might well represent any sort of species. The following should reinforced as standards: *Shorea almon* as *almon*, *S. polysperma* as *tangile*, and *S. palosapis* as *mayapis*. In Malaya and Borneo the group is represented by *nemesu* itself, *Shorea pauciflora*, and in Borneo by a difficult group of species that surround *S. smithiana*. Whereas *nemesu* has a scaly or square-fissured bark and a dark purple-red inner bark (a dark red meranti timber), *S. smithiana* has a Mutica-like deeply fissured bark and a light red timber.

**A - *Shorea*: Mutica Group - a**  
*Shorea* section *Mutica*

**A -- *Shorea*: Nemesu-Tangile Group -- a**  
*Shorea* section *Brachypterae*

This group includes about 100 species distributed chiefly in the Sundaic Region, centered in Borneo (60 species) and Malaya (23 species) with a few species reaching the

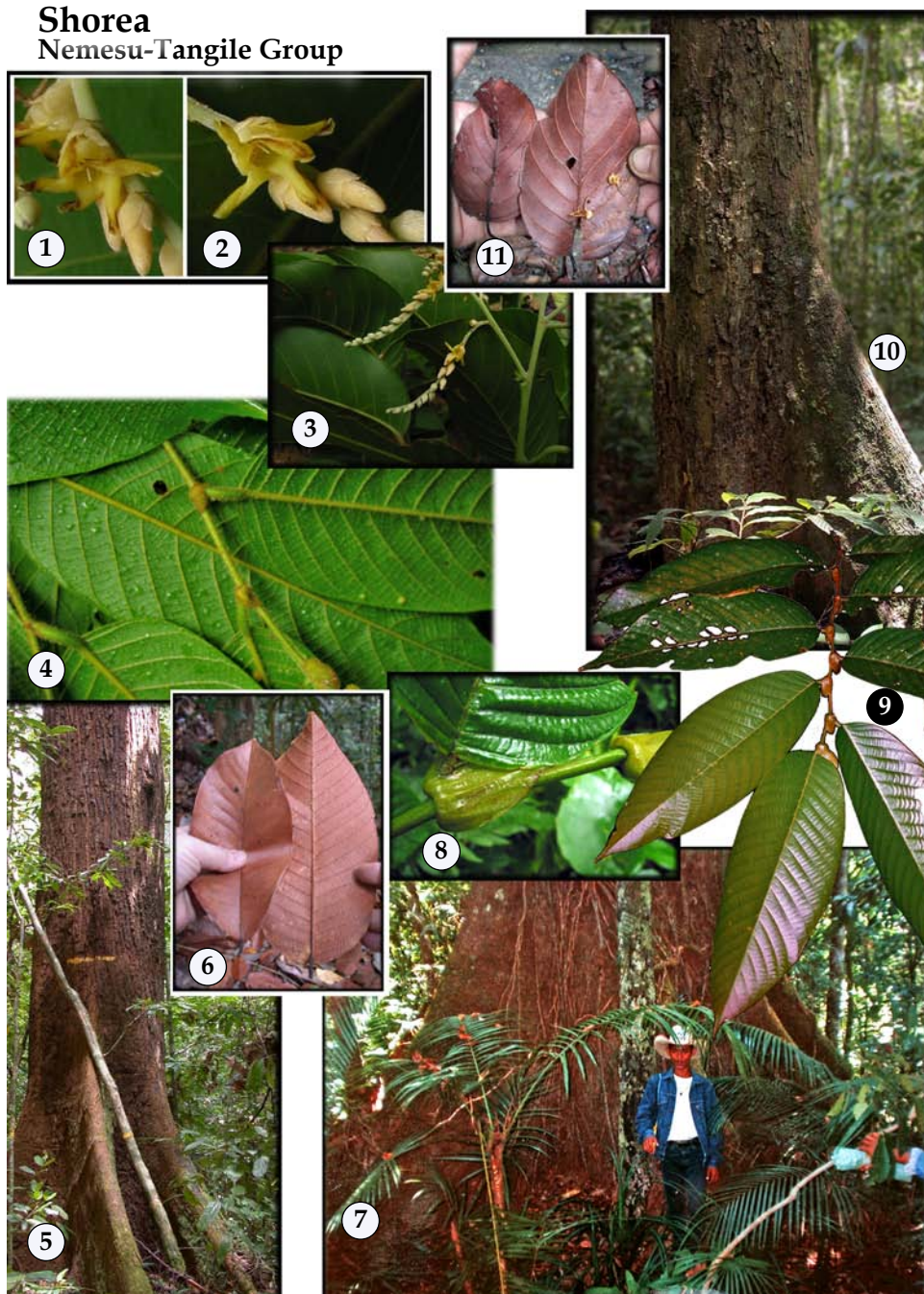
## Shorea ovalis



*Shorea ovalis*. 1, the crown of a fast-growing individual, in 1985 it was 7 cm DBH, in 2005, 22 cm DBH; 2, the fallen dry leaf is characteristically elliptic with many strong regular nerves and a curved boat shape; 3, the more oblong leaf characteristic of the Sarawak population; 4, the juvenile leaf with stipules inflated, constricted at the base and persistent; 5, bark of a mature tree with pale resin.

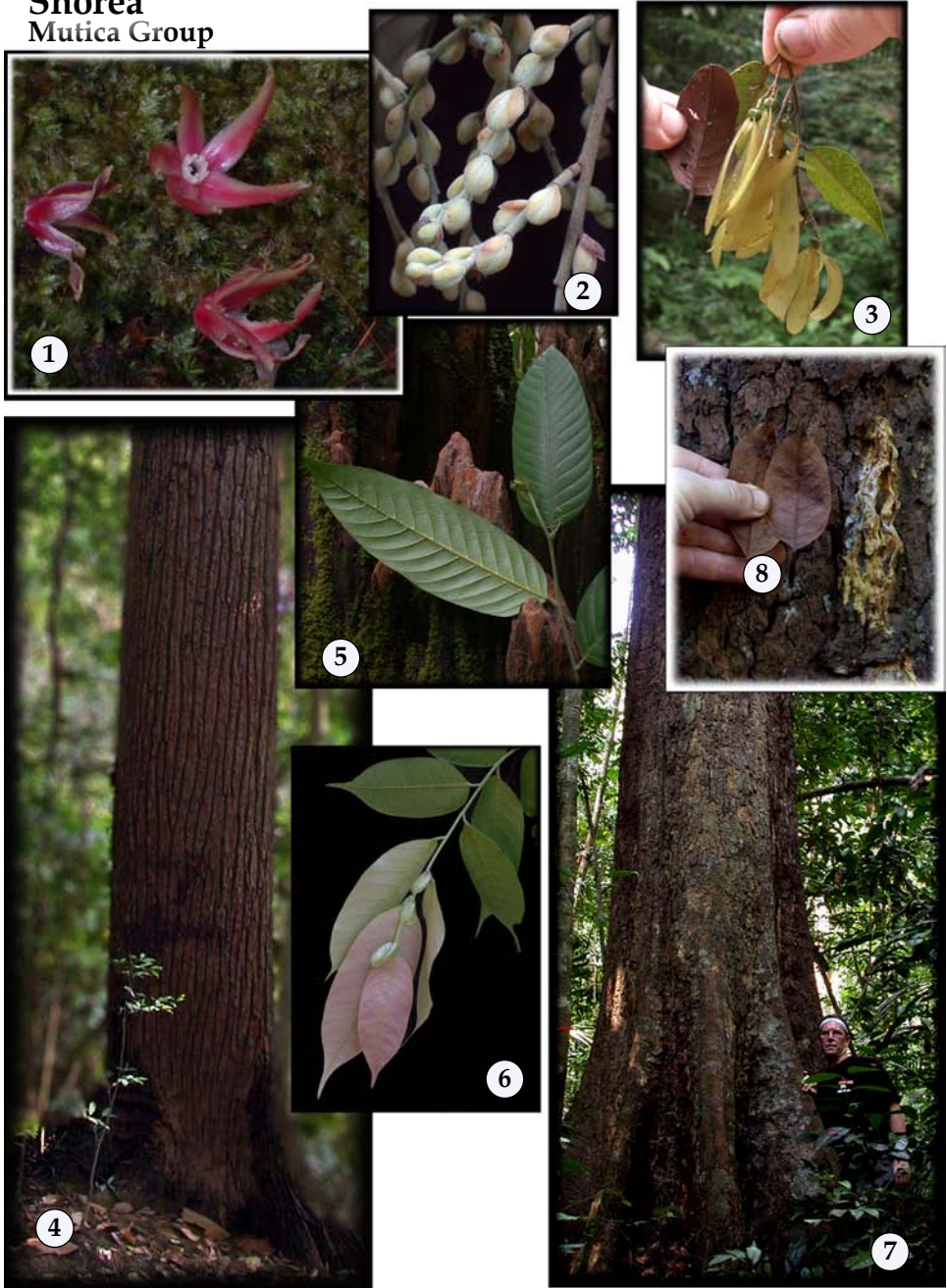


## Shorea Nemesu-Tangile Group



*Shorea*: Nemesu-Tangile Group. 1-3, *Shorea polysperma*, flower and inflorescence; 4, *S. almon*, juvenile, with short stalk, strong raised nerves, strong persistent stipules; 5, *S. smithiana*, a different type of bark, nearly fissured, the leaves large and broad; 7, a very large diameter *S. palosapis*, Palanan, Philippines, a tree of large diameter but no more than 35 m tall; 8, *S. palosapis* juvenile, with persistent inflated and constricted stipules; 9, the leaf of the juvenile; 10-11, *nemesu*, *Shorea pauciflora*; 10, with a square cracked to shaggy bark; 11, the leaves smooth and broadly elliptic, here with fallen corollas. (1-4, 8 & 9 © Leonardo L. Co.)

# Shorea Mutica Group



*Shorea Mutica* Group. 1, when trees are in flower, the fallen corolla litter the forest floor beneath large trees every morning; flowers are about 10 mm across with 15 stamens fused to the base of the corolla; 2, *S. leprosula* flower buds; 3, the fruit are of various sizes, some small as in *S. parvifolia*, but uniformly with three wings; 4, many species of the Mutica Group have a dark red deeply fissured bark as in *S. curtisii*, Bukit Timah, Singapore; 5, the leaf bears strong regular nerves arched and fading to the margin, with numerous and closely spaced scalariform veins, distinctive to species in details, as in *S. leprosula* the lower leaf bears a row of domatia along the mid-rib; 6, the stipules of Mutica Group are often large and persistent, and diagnostic to species, *S. acuminata*; 7-8, another common bark form in the group, here *S. acuminata*, with low buttresses, flaky dark brown bark, with patches of white resin crusted on the trunk.





*Shorea macroptera* is a common and widespread species and represents a different kind of species in the Mutica Group in that the bark is smooth rather than fissured (tree 49 cm DBH), the leaves are long, elliptic and with less conspicuous scalariform venation, drying nearly smooth. The three calyx lobes that expand as wings are red, as is typical of many species of *Shorea*; note that the dry fruit to the right has one of the wings behind the others.

southern Thai Peninsula and a few species in the Philippines, but not in Sulawesi or farther east. The name *red meranti* is a timber name and roughly synonymous with the group, but other timber names are sometimes used including: *seraya*, and *lup* (Iban) and *red lauau* (Philippines) for soft-woods, and the Iban *perawan* for harder woods. These are all medium to large trees, buttresses large, thick rounded, outer bark variable but often with dammar exuded, inner bark red to orange, soft, the outer bark is characterized by a deep and sharp v-shaped furrows. However, *Shorea macroptera* and allies have a relatively smooth bark that breaks off in plates.

The Mutica Group comprises fast-growing, high light-demanding species that can adapt to both plantation conditions and to silvicultural treatment. They famously flower at irregular intervals of four to 11 years, all synchronously within a species - at least within a local geographic province - and each species in a particular sequenced order. Wood boring beetles are a nuisance to many species, and 'shot holes' often make the wood less than perfect for furniture. Weevils are a very destructive pest of the young flowers. The female weevil lays an egg in each ovary; as the young larva grows and feeds it often destroys the plant embryo. The fruits that litter the ground below the mother tree may appear to be healthy but are without a viable embryo. The lives of these weevils in the periods between the mast fruiting events is



*Shorea rubella* represents the Negrosensis Group, a small group distinguished by floral details, the species are individually distinctive, here with a scaly black bark and the leaves with few strongly ascending nerves against a pale tannish lower surface.

still poorly understood, but they can be kept alive on banana, so presumably they have other means for feeding and reproducing. There are so many well-known and important species in the group, that we must resist the temptation to begin a list, but we might mention two.

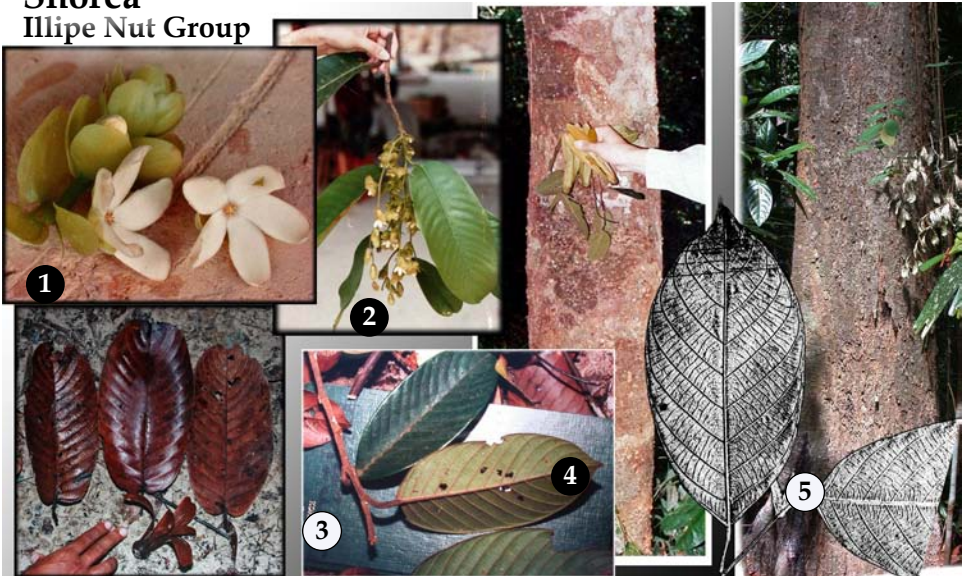
*Shorea curtisii* is the abundant hill *seraya*. In the Malay Peninsula it forms distinctive populations along the edge of steep ridges, conspicuous from above because of the peculiar blue-green sheen of the canopy. These are the trees that give Bukit Timah, Singapore its characteristic facade. Because its ecology is so uniform in the Peninsula, it is surprising that in west Borneo *seraya* can grow in more ordinary populations along flat terrain.

*Shorea leprosula* is widespread in the Sundaic Region and well-known as *meranti-tembaga*, on account of the coppery appearance of the foliage when viewed from below. The lower leaf bears a diagnostic set of domatia in the nerve axils along the midrib. It is among the fastest-growing of dipterocarps and a critical element in gap regeneration.

#### A -- *Shorea*: Illipe-Nut Group -- a *Shorea* section *Pachycarpa*

This group includes about 10 species of Borneo, apparently closely related, sometimes hybridizing, distinguished by the filaments which are more or less fused around the ovary. The names *engkabang*, *kawang* and *tengkawang* are given to the trees, which produce a *red meranti* timber and also the *illipe* nut of commerce. The

**Shorea**  
**Illipe Nut Group**



*Shorea* Illipe-Nut Group. 1-3, *S. macrophylla* Borneo; 1-2, flower, and inflorescence; 3, fallen leaf and fruit with large seed and short broad calyx wings; 4-5, *S. amplexicaulis*, Sarawak.

**Shorea**  
**Balau Group**



Balau Group. 1-2, *Shorea falciferoides*, Sarawak; 1, a very large tree, 148 cm diameter above the buttresses; 2, the fallen leaf, ordinary *Shorea* type, papery with numerous regular nerves, a bit glaucous silvery below; 3-4, *Shorea maxwelliana*, Malay Peninsula, the leaf of the juvenile, very small stipule, broadly spreading main nerves; 4, the trunk of a juvenile tree, 8 cm DBH; 5, flowers of *Shorea malibato*, Philippines. (Photograph 5, © Edwino S. Fernando).



fruit contains up to 70% fat with such a high melting point that it has become a preferred base for chocolates and cosmetics. Small-scale plantations have been attempted in Sarawak aimed at both fruit and timber.

### A -- *Shorea negrosensis* Group -- a

A group of five species, Borneo and the Philippines, questionably monophyletic, with two critical species: *Shorea albida*, the classic tree of monospecific peat swamp forests, with numerous local names depending on the disposition of the tree, but especially *alan*. The second important species is *Shorea negrosensis*, found widely in the Philippines as *mangachapui*; it yields a red *lauan* timber.

### A -- *Shorea*: Balau Group -- a

*Shorea* section *Shorea*

Species richness is highest in Borneo with about 20 species, but those few species found in dry-seasonal lands are also abundant. Note that *balau* is a timber name as well, and can be applied to the timber of unrelated species in *Shorea* and *Hopea*. This type of tree is well-known everywhere in tropical Asia, the timber valued for its weight and strength: *selangan batu* in Borneo, *balau* in Malaya, *guijo* or *yakal* in the Philippines.

These are often beautiful big trees with sharp buttresses, a cracked or scaly bark, not with regular fissures. In the forest, they will look very much like some of the species of *Hopea* section *Hopea*, and diagnostic vegetative differences are lacking. These are among the most potentially valuable timbers trees. They were much sought after when heavy woods were needed for railroad and other heavy construction. But the wood is tight and hard and can be difficult to nail and so today the trees are sometimes left uncut in the forest.

Included here is the *sal* tree, *S. robusta*, the most abundant dipterocarp species in Central and N India, Nepal, Burma, and parts of Thailand, forming near monospecific stands, or mixed with other species, widely used in regeneration. According to folklore, the Nepalese temple of Kasthamandap is made from a single giant *sal* tree. Also, by legend, it was under the shade of a *sal* tree that Buddha was born.

### A -- *Shorea*: Yellow Meranti Group -- a

*Shorea* section *Richetioides*

The group includes about 35 species. Molecular evidence indicates all are closely related and strongly monophyletic. A few of the species are known as *meranti damar hitam* in reference to the black resin typically encrusted on the bole, or in Iban as *lun* for soft-wooded species, *barek* for hard wooded. Essentially trees of the Sunda Shelf lowland forest, not reaching the seasonal forests of Indo-Burma. Small to large trees, variable buttresses, the outer bark at first chocolate and gray dipped, irregularly

cracked and flaked, not deeply furrowed or fissured like the red merantis, usually with abundant old black dammar. The inner bark is yellow, never laminated as it is in the white merantis. The wings of the calyx are often reduced. Some of the species - *Shorea laxa*, most famously - regenerate exceedingly well with dense carpets of seedlings and saplings under foot. The leaves often retain a yellow-green color when dry. These trees are not so abundant as the red meranti but are often numerous along the slopes of hilly forests over 100 m, and are not found much at all in swampy ground.

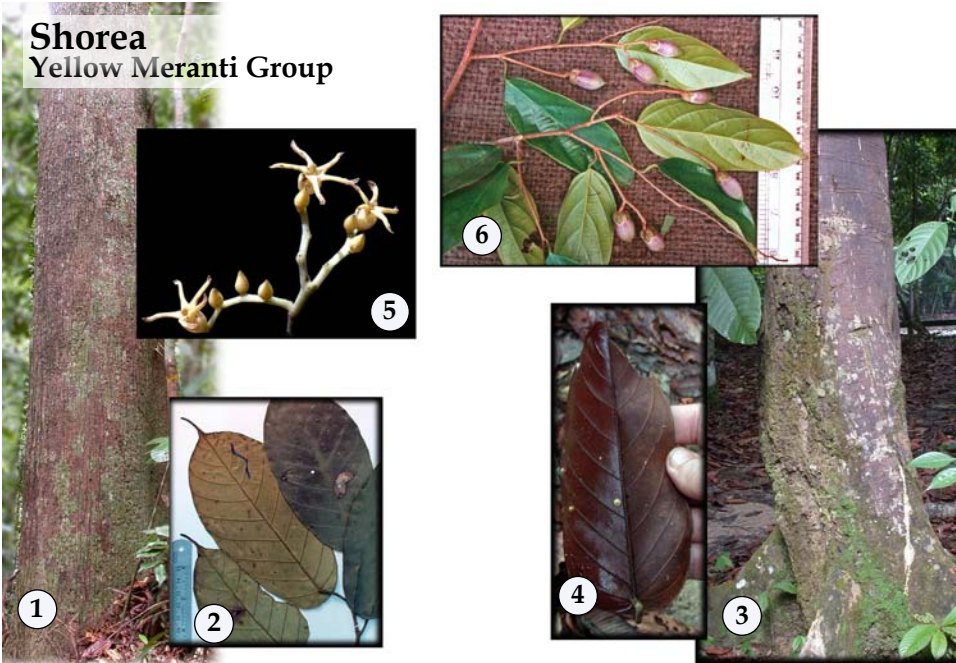
### A -- *Parashorea* Group -- a

**PARASHOREA.** [Greek, near or like *Shorea*.] A group of about 14 species, distinguished from other genera in the Shoreae tribe by plicate leaves often with a glaucous lower surface, by the calyx lobes being nearly valvate in bud and all expanding roughly equally in length, and by the globose and warty fruit. In the light of those distinctive features, the generic status of *Parashorea* is surprisingly equivocal. In the first molecular study that included more than one species, Indrioko *et al.* (cited above) found that *P. lucida* and *P. globosus* failed to pair at all. A recent molecular study of the former *Shorea chinensis* found 80% boot-strap for its return to *Parashorea* rather than remain in *Shorea* where it had been transferred<sup>21</sup>. And in an UPGMA clustering of AFLP fragments, Cao found that *P. lucida* and *P. globosa* clustered as sister taxa, but with less than 50% bootstrap support<sup>22</sup>. All of this is surprising to field biologists familiar with these distinctive species.

No single species is especially widespread, but at least one is found in any particular lowland forest in tropical Asia with the exception of Java, the Lesser Sunda Islands and Sulawesi. To the far northwest, the genus is represented by *Parashorea chinensis*, an ecologically critical species in Xishuangbanna. In Mainland SE Asia, we find two narrowly distributed species, and also *P. stellata* which reaches northern Malaya, and *P. lucida* which extends into Sumatra. Several other species occur in Borneo and are endemic to that island. Most often, the species of the Sundaic Region are relatively sparse in abundance, so much so that they never make a major contribution to the timber market. But to the north and east the situation differs. *Parashorea malaanonan* of the Philippines reaches NE Borneo where it coincides with the presumed sister species *P. tomentella*. Together these two species were the source of a *lauan* timber in the Philippines and in Sabah as *urat mata* or *white seraya*, which in volume of export was second only to the 20 or 30 species comprising the Red Merantis. The special ecological features of *Parashorea* that contribute to this local dominance remain unexplained, as does the absence of the genus to the south and east.

<sup>21</sup>Li, Q. *et al.* 2004. Taxon. 53: 461-466.

<sup>22</sup>Cao, C. 2006. Genetic variation of the genus *Shorea* (Dipterocarpaceae) in Indonesia. Dissertation. Doctor of Forestry Science at the Faculty of Forest Sciences and Forest Ecology. Georg-August University of Göttingen.



*Shorea*: Yellow Meranti Group. 1-2, *S. laxa*, Sarawak, 70 cm DBH; 2, the papyery peltate leaf; 3-5, *S. maxima*, Malay Peninsula, with a smooth hooped bark and whitish dammar; 4, papyery leaf, ordinary *Shorea* venation; 5, flower; 6. *S. dolichocarpa*, Sarawak, many, though not all, species of yellow meranti bear wingless fruit.



*Parashorea*. 1-2, *P. densifolia*, Malay Peninsula; 1, juvenile and adult leaf, 3. *P. parvifolia*, Sarawak, nearly identical form of bole to the Malayan tree; 4, *P. malaanonan*, Philippines (© Nestor Bartolome); 5, *P. lucida*, Peninsular Thailand.

Comparison of field groups and taxonomic sections of *Hopea*.

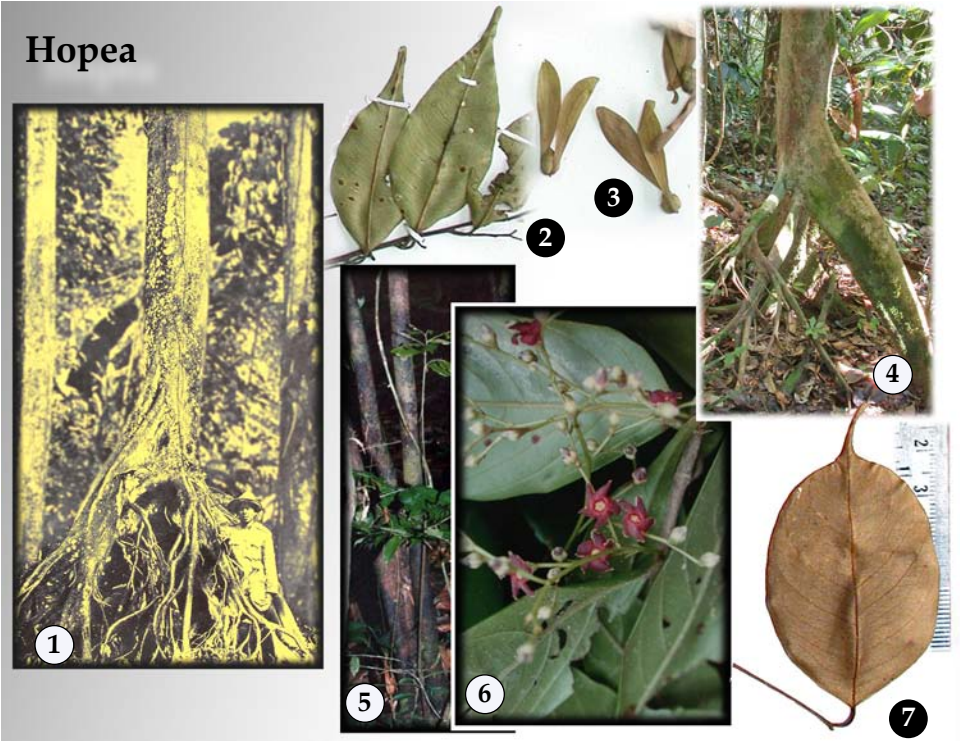
Taxonomic Sections	FIELD GROUPS			
	Smooth-barked	Mata Kuching	Fissured bark	Scaly bark
Section <i>Hopea</i> subsection <i>Hopea</i>				<i>H. ferrea</i> <i>H. odorata</i> <i>H. sangal</i> <i>H. acuminata</i>
Section <i>Hopea</i> subsection <i>Pierrea</i>	<i>H. apiculata</i> <i>H. glaucescens</i> <i>H. polyalthioides</i> <i>H. pterygota</i>			
Section <i>Dryobalanoides</i> subsection <i>Dryobalanoides</i>	<i>H. dyeri</i> <i>H. griffithii</i>	<i>H. ferruginea</i> <i>H. johorensis</i> <i>H. latifolia</i>	<i>H. mengarawan</i>	
Section <i>Dryobalanoides</i> subsection <i>Sphaerocarpace</i>	<i>H. nervosa</i>			<i>H. sublancoolata</i>

A -- *Hopea* Group -- a

HOPEA. [Commemorates John Hope d. 1786, Professor of Botany at Edinburgh.] A heterogeneous group of about 105 species, distributed from India and Sri Lanka to S China, Borneo Philippines and New Guinea. Most species have a two-winged fruit and so differ from *Shorea* which usually has three-winged fruit. However

in details of leaf and bark, species of *Hopea* are highly varied.

Symington recognized four different kinds of *Hopea* which he called field groups. They have an overlapping relationship to the four taxonomic sections recognized by Ashton in the treatment for *Flora Malesiana*, as illustrated in the table. The four field groups can be described as follows:



*Hopea*. 1, *H. mengarawan*, Malay Peninsula circa 1927, with characteristic prop roots; 2-3, *H. dyeri*, fine dryobalanoid venation and 2-winged fruit about 3 cm long; 4, *H. mengarawan*, a small tree with arching prop roots; 5-6, *H. wyatt-smithii*, Lambir, Sarawak, a species of very small stature, typically with several thin trunks, black bark; 7, *H. beccariana* with dryobalanoid venation.



# Hopea



*Hopea*. 1, *H. acuminata*, Luzon, Philippines, with characteristic domatia in lower leaf axils; 2, *H. pterygota*, Lambir, Sarawak, with strong raised nerves and 2-winged fruit; 3, *H. odorata*, Huai Kha Khaeng, Thailand, the most abundant of large canopy trees.

Smooth-barked Group - small and medium trees, often with stilt roots, with smooth bark and without obvious exuded dammar; the leaves scalariform or dryobalanoid, timber is a merawan type.

Mata Kuching Group - trees as in the smooth barked group but with conspicuous masses of exuded dammar; the are dryobalanoid, the timber of the merawan type.

Fissured Bark Group - as in the Smooth Bark group but with a deeply fissured bark, the leaves are dryobalanoid, the timber is of the merawan type.

Scaly Bark Group - the most distinctive of the four groups, although can be confused in the field with *balau* types of *Shorea*, often large trees without stilt roots, scaly dark bark, leaves with scalariform venation, the timber a heavy hardwood.

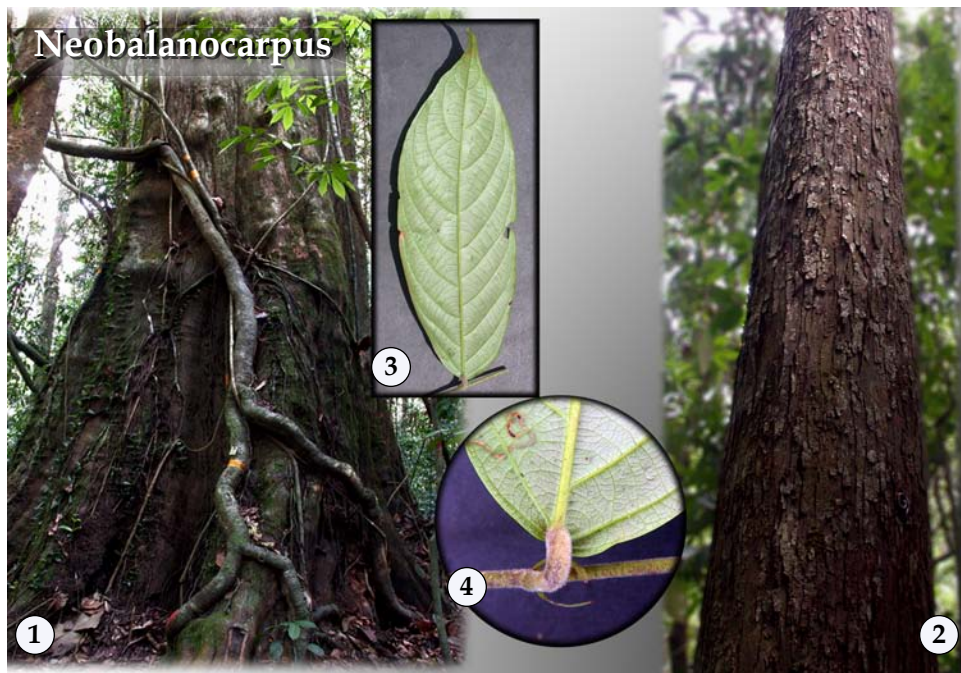
## A -- *Hopea* sect. *Dryobalanoides* -- a

This is a large heterogeneous section but includes all of the species of *Hopea* with distinctive dyobalanoid venation, and also all of those with the equally distinctive mass of prop roots. The many permanent plots established during the last century tell a similar story with regard to these kinds of *Hopea*. The adult trees are typically found in the center a great carpet of 1-2 cm DBH saplings that spread out in a patchy population perhaps



*Hopea odorata*, planted along a street in Ho Chi Minh City, Vietnam, trees range from 60-100 cm DBH, most are between 80 and 120 years old.





*Neobalanocarpus heimii*, Pasoh, Malaya; 1, a very large tree, nearly 300 cm diameter at ground level; 2, a younger tree with characteristic bark; 3-4, the leaf with tiny cat-whisker stipules and asymmetric leaf base.

100 m or more across. These dense patchy populations appear to persist a relatively short time. EJ Corner established a permanent plot in Bukit Tliah Singapore in the 1930s, and although the data have never been found, the voucher specimens from individual trees stored in the Singapore herbarium indicate that *Hopea griffithii* was among the most abundant species. It is today represented by only a few old trees and no saplings, while new dense populations are common in the Central Catchment several km away. The large-scale plots are only 20-30 years old, but they indicate that these populations, so obvious among the mapped distributions, are likewise exceedingly dynamic.

#### A -- *Hopea* sect. *Hopea* -- a

These are the most distinctive of the species of *Hopea*, and they also include many of the more abundant and ecologically important species. The share with other *Hopea* a two-winged fruit; they differ in the strongly scalariform leaf venation, often with domatia in the nerve axils, in the dark scaly bark of the mature tree, the lack of prop roots, and in the very hard heavy timber. The species *H. odorata* and *H. ferrea* are among the most important dipterocarps of the dry seasonal parts of Mainland SE Asia, and also India. *Hopea odorata* was among the most abundant of large trees in the evergreen forests of Huai Kha Khaeng Thailand, and although it flowered and fruited routinely, it was sparsely represented by juveniles and recruits. *Hopea acuminata* is the widespread Philippine endemic known as *manggachapui*, formerly abundant in most Philippine islands.

#### A -- *Chengal* Group -- a

**NEOBALANOCARPUS.** [A name coined to replace the invalid *Balanocarpus*, Greek for acorn fruit, in reference to the wingless fruit.] A genus of one species, *Neobalanocarpus heimii*, well-known throughout the Malay Peninsula as *chengal*. This is among the largest of dipterocarps, and among the largest of all tropical Trees, as well as the only really big dipterocarp with wingless fruit. It is patchily distributed in the Malay Penin-



The traditional palace at Sri Menenti, Negri Sembilan, Malaysia, built in 1917, entirely of *chengal* timber.

sula, but where it occurs it is often abundant. The acorn-like fruit fall in abundance more regularly than in other dipterocarps. More than 3500 saplings were recorded in the Pasoh plot, their spatial distribution was complex with a fair degree of evenness marked by numerous dense patches. This species combines morphological features of *Hopea* and *white meranti* and there is some evidence (in the cited molecular studies) that it represents an ancient hybrid. Trees larger than 10 cm DBH routinely grow more than 0.5 cm DBH per year. The timber is among the most valuable in Malaya.

**A -- *Pentacme* Group -- a**  
*Shorea* section *Pentacme*

Two important species were formerly segregated as *Pentacme*. Ashton in *Flora Malesiana* treats them as a section of *Shorea* whereas Maury-Lechon, cited above, associated these two species with *Shorea* section *Anthoshorea* as well as the Sri Lankan endemics formerly



*Shorea contorta*, formerly *Pentacme contorta*, endemic to the Philippines, the leaves are broad and smooth with arched nerves; the wood is of the white meranti timber type, in the Philippines called white luan.



*Shorea siamensis*, formerly *Pentacme siamensis*, distinctive in the large leaves with slightly invaginate base, here at 800 m elevation in central Vietnam.

of the genus *Doona*, in a broadly defined white meranti group. The two species of *Pentacme* are quite divergent from one another and from other species of *Shorea* as well. They have not been the subject of molecular studies and it is possible, perhaps likely, that *Shorea siamensis* is allied with neither *Shorea contorta* nor with the white merantis of section *Anthoshorea*.

*Shorea siamensis* (formerly as *Pentacme siamensis*) is a distinctive and common tree of Mainland SE Asia, reaching as far south as northern Malaya. It is deciduous species, large-leaved with a nearly cordate leaf base, sometimes of large stature, but often small and gnarled, yielding a very heavy timber. In eastern Thailand and Cambodia it forms a particularly distinctive forest type when associated with *Hopea ferrea*. *Shorea contorta* is a Philippine endemic, with a softer *white luan* timber, formerly widespread and abundant in most Philippine islands.

**A -- White Meranti Group -- a**  
*Shorea* section *Anthoshorea*

The White Meranti group includes about 30 species from Sri Lanka to Borneo. These are large trees with variable buttresses; the pale yellow inner bark is laminated, a feature shared only with *Anisoptera*. The bark is irregularly fissured, sometimes smooth;



## Shorea ochracea



*Shorea ochracea*, Lambir, Sarawak, somewhat isolated species of the section *Anthoshorea*, the white *meranti* group, with distinctive and readily identifiable leaves and bark.

the wood is soft to medium hard with a coarse texture; the dammar is pale yellow. The group includes the very widespread *Shorea assamica* distributed from India to the Philippines. *Meranti pa'ang* is the name of the best known Malayan member, *Shorea bracteolata*, which is then given to the whole group. The name *melapi* is common in North Borneo, while the Iban is *raru* or *raruk* and especially for the remarkably distinctive *Shorea ochracea*. The relationship of this group to *Doona* of Sri Lanka and *Pentacme* is still to be resolved.

## Shorea bracteolata



*Shorea bracteolata*, a white *meranti*, distinctive in the large white cup-shaped flowers, the elliptic leaves that curl boat-shaped as they gather on the ground.